

A group of two: *Scapter peringueyi* is not a synonym of *Scapter heterodoxus* (Hymenoptera, Colletidae, Scraptrinae)

Silas Bossert^{1,2}, Simon van Noort^{3,4}

1 Department of Entomology, Washington State University, Pullman, WA, 99164, USA **2** Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA **3** Research and Exhibitions Department, South African Museum, Iziko Museums of South Africa, Cape Town, 8000, South Africa **4** Department of Biological Sciences, University of Cape Town, Private Bag, Rondebosch, 7701, South Africa

Corresponding author: Silas Bossert (silas.bossert@wsu.edu)

Academic editor: D. Brothers | Received 25 October 2021 | Accepted 30 December 2021 | Published 21 January 2022

<http://zoobank.org/CB17C6B2-CF80-4B11-A100-E340E5CB66A2>

Citation: Bossert S, van Noort S (2022) A group of two: *Scapter peringueyi* is not a synonym of *Scapter heterodoxus* (Hymenoptera, Colletidae, Scraptrinae). African Invertebrates 63(1): 1–18. <https://doi.org/10.3897/AfrInvertebr.63.76934>

Abstract

Scapter is a genus of colletid bees with a primary distribution centered in Southern Africa. The genus currently comprises 68 recognized species, which are divided into nine species groups, ranging from one to 29 included species. The *Scapter heterodoxus* group is presently considered to be the only monotypic group, because of synonymization of *Scapter heterodoxus* with *Scapter peringueyi* in a previous revision of the genus. A comparative examination of these two species using both morphological assessment and molecular sequence data from the COI barcode region supported the recognition of *S. peringueyi* as a valid species, which we accordingly resurrect as the second species of the *Scapter heterodoxus* species group. We provide high resolution images of the type specimens for both species and updated diagnoses to enable their separation from all other species of *Scapter*.

Keywords

Bees, COI, DNA barcoding, Afrotropical, morphology

Introduction

Scapter Lepeletier & Serville, 1828 is a genus of colletid bees endemic to Africa (Eardley 1996; Davies et al. 2005; Michener 2007; Eardley et al. 2010). A species-rich genus, *Scapter* currently comprises 68 recognized species (Kuhlmann and Friehs 2020), and new species are being discovered at a remarkable pace. In the past 25 years since Eardley's (1996) revision of the genus, in which he recognized 31 valid species, more than 30 new species have been described (Davies et al. 2005; Davies and Brothers 2006; Kuhlmann 2014; Kuhlmann and Friehs 2020). As many species of *Scapter* seem to be ephemeral in their biology, including tight hostplant associations and narrow flight periods in highly seasonal environments (Kuhlmann 2009; Kuhlmann and Eardley 2012; Kuhlmann et al. 2012; Kuhlmann and Friehs 2020), this increase of newly discovered species can be expected to continue into the upcoming decades.

In the past, the phylogenetic relationships of *Scapter* to other colletid lineages proved difficult to establish based on morphology alone (McGinley 1981; Alexander and Michener 1995; Plant and Paulus 2016). Previously considered to be part of Paracolletini (e.g., Michener 1944), albeit without strong morphological evidence (McGinley 1981), analyses of nucleotide sequence data strongly indicated a sister group relationship of Scraptrinae and Euryglossinae, an Australian-endemic lineage of Colletidae (Almeida and Danforth 2009; Almeida et al. 2012; Kayaalp et al. 2017; Cardinal et al. 2018). Interestingly, a close relationship to Euryglossinae has been discussed as early as 1933 (Cockerell and Ireland 1933; specifically discussing *Euryglossidia* Cockerell) and a sister-group relationship is supported by certain morphological characters of the mature larvae (McGinley 1981). Fossil-based divergence-time estimates agree that the lineages forming the present-day Scraptrinae and Euryglossinae split in the early Eocene, around ~55 million years ago (Almeida et al. 2012; Kayaalp et al. 2017). *Scapter* is the only colletid lineage endemic to Africa, and with the exception of one species reported from Kenya (Davies et al. 2005), it is geographically restricted to southern Africa. With Euryglossinae being endemic to Australia, the biogeographical puzzle leading to this exceptional distribution has been difficult to explain (Almeida et al. 2012; Kayaalp et al. 2017).

Scapter is a morphologically heterogeneous genus (Davies and Brothers 2006) with great differences in body size (e.g., 3.5 mm, *Scapter minutissimus* Kuhlmann, 2014 vs. 14 mm, *Scapter heterodoxus* (Cockerell, 1921)). Eardley (1996) presented the first attempt to systematically revise the genus, including redescriptions, synonymizations, and type designations. He established eight species groups based on similar characteristics, and Kuhlmann (2014) added the 'euryglossiform' species as a ninth group. One group, the *Scapter heterodoxus* group is currently understood as being monotypic, because Eardley (1996) synonymized *Scapter peringueyi* (Cockerell, 1921) with *Scapter heterodoxus*. Both these species were described by Cockerell (1921) in the same article, but based on different sexes. In the present article, we re-examine the type specimens of the two species and additional material of the *Scapter heterodoxus* group. Studying both sexes of both species, we found strong morphological evidence that *S. peringueyi* is not a synonym of *S. heterodoxus*, but a valid species.

Nucleotide sequence data from COI barcodes of both morphotypes show a divergence of > 6%, underlining the significant discrepancy between the two lineages. Based on this combined evidence, we resurrect *S. peringueyi* as a valid species.

Materials and methods

We located and examined the type specimens of *S. heterodoxus* and *S. peringueyi* in the collections of the Iziko South African Museum, Cape Town (**SAMC**), and in the South African National Collection of Insects, Pretoria (**SANC**). Additional specimens of both species were collected during field work by Bryan Danforth in South Africa in September 2001 and were deposited in the Cornell University Insect Collection (**CUIC**). In total, we examined 133 specimens, which includes all specimens deposited in the collections of the SAMC and the CUIC. We mapped the distributions of the two recognized species using SimpleMappr (Shorthouse 2010). The terminology of surface sculpturing follows Harris (1979).

To compare the DNA sequences of *Scapter heterodoxus* and *S. peringueyi*, we obtained sequence data for both species. One COI sequence for *S. heterodoxus* was retrieved from GenBank (identifier [MH578427](#)) and we extracted another COI barcode from a UCE assembly of the same species (from Branstetter et al. 2017). This DNA sequence data is associated with a male voucher specimen which is deposited in the CUIC. This voucher specimen was examined in the present study and is part of a series of specimens consisting of male and female *S. heterodoxus*: males and females were collected jointly at the same time and place. Since both sexes share distinct morphological features that distinguish them from what was described as *S. peringueyi*, we deemed them conspecific. For *S. peringueyi*, we generated two new barcode sequences. Two male specimens collected on 28 September 2001 and listed below under additional material were used for DNA extraction. These specimens are vouchered in the CUIC as well and are labelled with a green colored extraction code label. DNA was extracted from ground-up thorax tissue using a CTAB phenol-chloroform protocol. We used the DNA extractions to sequence ultraconserved elements (UCEs) as detailed in Bossert et al. (2021), as the *S. peringueyi* samples were processed jointly with the samples of that study. After assembling the raw read data with SPAdes (ver. 3.13.1; Bankevich et al. 2012), we extracted the COI barcode region using the script *phyluce_assembly_match_contigs_to_barcode*s of the Phyluce package (ver. 1.7.1; Faircloth 2016) and a reference COI barcode of *Apis mellifera* L., 1758. The four sequences consisting of two representative barcodes for each of *S. heterodoxus* and *S. peringueyi* were aligned with MUSCLE (ver. 3.8.425; Edgar 2004).

Examination of the sequence alignment by eye revealed that for each species the two barcode sequences differed in length but were otherwise identical across the shared positions. Since we were interested in examining the interspecific distance between *S. heterodoxus* and *S. peringueyi*, we only retained the longest DNA sequence for each species. This led to a sequence alignment of 658 nucleotides (658 present positions for *S. heterodoxus* and 657 for *S. peringueyi*). We estimated the evolutionary distance

between these two sequences by quantifying the proportion of sites at which nucleotides differed (*p*-distance). We uploaded the reference COI sequence of *S. peringueyi* to NCBI GenBank where it can be retrieved under identifier MZ682106. The sequence alignment of all four sequences can be found as Suppl. material 1.

Images were acquired at SAMC with a Leica LAS 4.9 imaging system, comprising a Leica Z16 microscope (using either a 2× or 5× objective) with a Leica DFC450 Camera and 0.63× video objective attached. The imaging process, using an automated Z-stepper, was managed using the Leica Application Suite V 4.9 software installed on a desktop computer. Diffused lighting was achieved using a Leica LED5000 HDI dome. All images presented in this paper, as well as supplementary images, are available on WaspWeb at www.waspweb.org.

Depositories

- CUIC** Cornell University Insect Collection, Ithaca, NY, USA.
SAMC South African Museum, Iziko Museums of South Africa, Cape Town, South Africa.
SANC National Collection of Insects, Pretoria, South Africa.

Results

Systematics

Subfamily Scapttrinae Ascher & Engel, 2005

Genus *Scapter* Lepeletier & Serville, 1828

Scapter Lepeletier & Serville, 1828: 403 (not *Scapter* Lepeletier, 1841: 260). Type species: *Scapter bicolor* Lepeletier & Serville, 1828, by subsequent designation in Vachal (1897: 63).

Polyglossa Friese, 1909: 123. Type species: *Polyglossa capensis* Friese, 1909, by subsequent designation in Cockerell (1921: 203).

Strandiella Friese, 1912: 181. Type species: *Strandiella longula* Friese, 1912 = *Scapter niger* Lepeletier & Serville, 1828, by designation in Cockerell (1916: 430).

Polyglossa (*Parapolyglossa*) Brauns, 1929: 134. Type species: *Polyglossa heterodoxa* Cockerell, 1921, by subsequent designation in Sandhouse (1943: 584).

Comment. Michener (1997) clarified several problematic subsequent type designations.

Scapter heterodoxus (Cockerell, 1921)

Figures 1, 2, 5

Polyglossa heterodoxa Cockerell, 1921: 204.

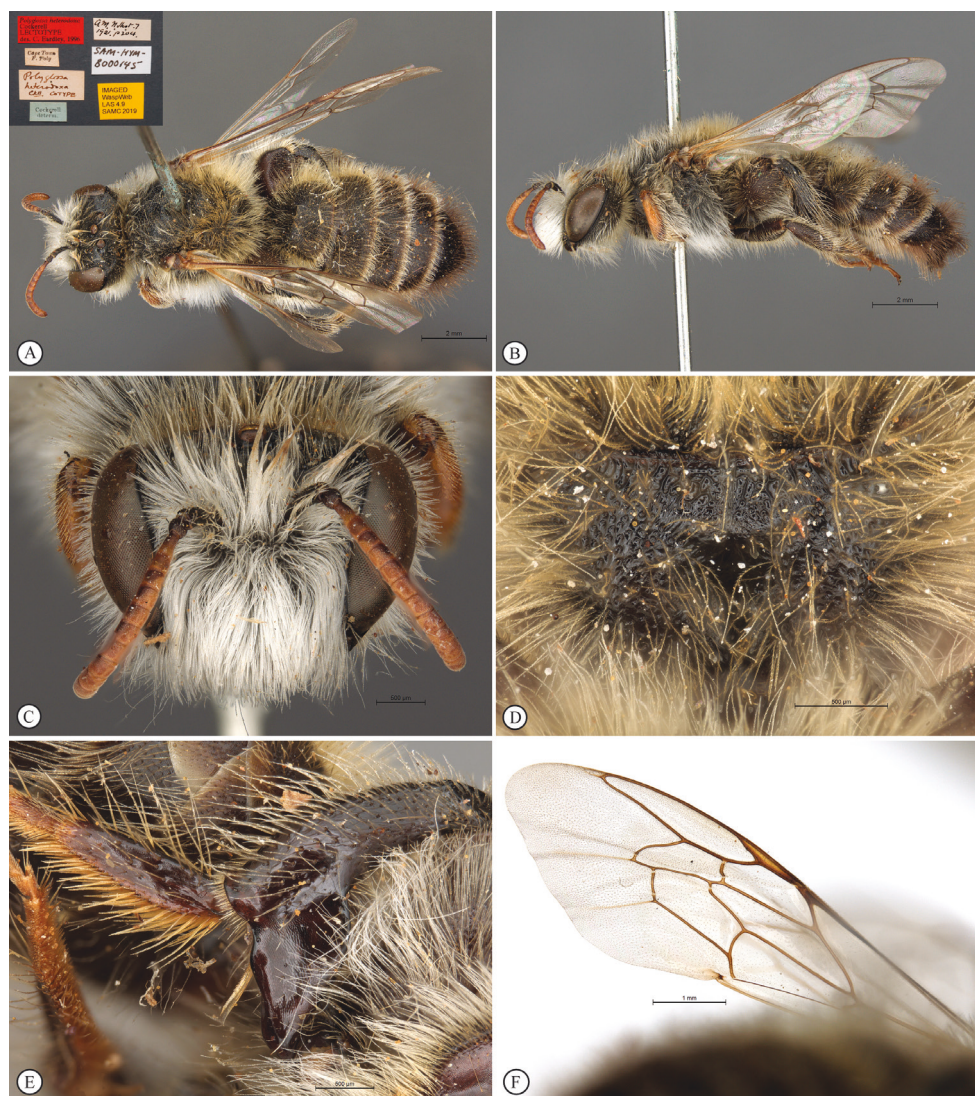


Figure 1. Male lectotype of *Scapter heterodoxus* (Cockerell, 1921). **A** habitus, dorsolateral view, and labels **B** habitus, lateral view **C** head, frontal view **D** propodeum **E** hind leg tibia **F** fore wing.

Material examined. Lectotype: South Africa: Cape Town, leg. F. Foly, ♂, SAMC, catalogue no. SAM-HYM-B000145. Labels associated with this specimen are shown in Fig. 1A. According to Cockerell (1921), the specimen was collected in 1914. Additional material: South Africa: Cape Province, 31 km S of Clanwilliam, 32°23.1'S, 18°56.8'E, 7 September 2001, leg. B. N. Danforth, C. D. Eardley, K. L. Walker, 6♂, 15♀, CUIC. Cape Province, Sauer, Suurfontein, -32.85, 18.5667, 25 August 1994, leg. V. B. Whitehead, 2♂, SAMC, cat. no. SAM-HYM-B007774. Cape Province, Holfontein, 20 km S. of Clanwilliam, -32.4333, 18.95, 8 August 1984, leg. V. B. Whitehead, 3♂, SAMC, cat. no. SAM-HYM-B007777. Cape Province, Piketberg, Witte-



Figure 2. Female non-type specimen of *Scapter heterodoxus* (Cockerell, 1921), (SAM-HYM-B007786). **A** habitus, dorsal view **B** habitus, lateral view **C** head, frontal view **D** propodeum **E** labels **F** fore wing.

water, -32.9167 , 18.7 , 5 September 1990, leg. V. B. Whitehead, 1♀, SAMC, cat. no. SAM-HYM-B007784. Cape Province, Piketberg, farm Hartbeesrivier, Kapteinskloof, -32.875 , 18.625 , 23 August 1991, leg. V. B. Whitehead, 1♂, SAMC, cat. no. SAM-HYM-B007785. Cape Province, Piketberg, Banghoek, -32.75 , 18.6 , 20 September 1991, leg. V. B. Whitehead, 1♀, SAMC, cat. no. SAM-HYM-B007786. Cape Province, Mamre, Malmesbury Div. Cape, -33.5167 , 18.4667 , 25 August 1977, leg. V. B. Whitehead, 1♂, SAMC, cat. no. SAM-HYM-B007788. Cape Province, Joostenbergkloof, Stellenbosch, -33.7667 , 18.7667 , 14 August 1988, leg. V. B. Whitehead, 3♂,

SAMC, cat. no. SAM-HYM-B007789. Cape Province, Joostenbergkloof, Stellenbosch, –33.7667, 18.7667, 31 July 1988, leg. V. B. Whitehead, 1♂, SAMC, cat. no. SAM-HYM-B007790. Cape Province, Katberg Pass, R351, –32.4667, 26.65, 25 November 1985, 1♀, SAMC, cat. no. SAM-HYM-B007791. Cape Province, Kakamas, 16.5 km N of Orange R. bridge, Rd to Namibia, –28.6000, 20.5667, 22 July 1993, leg. V. B. Whitehead, 1♀, SAMC, cat. no. SAM-HYM-B007792. Cape Province, Leipoldtville, –32.2333, 18.4833, 14 September 1984, leg. V. B. Whitehead, 2♀, SAMC, cat. no. SAM-HYM-B007793. Cape Province, Hetkruis, Groenrivier, –32.6, 18.75, 14 August 1991, leg. V. B. Whitehead, 1♂, SAMC, cat. no. SAM-HYM-B007794. Cape Province, 7 km N. of Elandsbaai, –32.25, 18.35, 21 September 1984, leg. V. B. Whitehead, 1♂ and 1♀, SAMC, cat. no. SAM-HYM-B007795. Cape Province, Doringfontein, 33km N. of Piketberg, 30 August 1987, –32.6, 18.7667, leg. V. B. Whitehead, 1♂, SAMC, cat. no. SAM-HYM-B007796. Cape Province, Tygerberg, –33.8833, 18.6, 14 September 1990, leg. K. Steiner, 1♀, SAMC, cat. no. SAM-HYM-B009506. Cape Province, Elands Bay, –32.3, 18.35, 26 September 1985, leg. V. B. Whitehead, 1♂, SAMC, cat. no. SAM-HYM-B009507. Cape Province, Sevilla, Traveller's Rest, –32.07278, 19.08056, 25 August 2007, leg. S. van Noort, 1♀, SAMC, cat. no. SAM-HYM-B010372. Cape Province, Somerset (W.) Strand, 25 October 1925, –34.1167, 18.8333, leg. H. Brauns, 1♀, SAMC, cat. no. SAM-HYM-B007776a.

Diagnosis. ♂: the male of *S. heterodoxus* differs from all other *Scapter* species except *S. peringueyi* in possessing the unique combination of the following characters: body size of ≥ 12 mm, hind femur greatly enlarged, hind tibia strongly broadened apically (Figs 1E, 5B), hind basitarsus unmodified (enlarged in *S. amplitarsus* Eardley, 1996) and midleg basitarsus unmodified (enlarged in *S. armatipes* (Fries, 1913)). *Scapter heterodoxus* differs from *S. peringueyi* in the shape of the apical section of the hind tibia: the shape of the projecting apical portion is tapering in *S. heterodoxus*, resembling a triangular shape, whereas the projecting apical portion of the tibia in *S. peringueyi* is parallel-sided, resembling a rectangular shape (Figs 1E, 4E, 5A, 5B). As in the female sex, the surface sculpturing of the basal zone of the propodeum is rugulose in *S. heterodoxus*, whereas it is substrigulate in *S. peringueyi* (Figs 5C, 5D). The integument between the punctuation on the mesoscutum is polished in *S. heterodoxus* and shagreened (dull) in *S. peringueyi*.

♀: The female differs from most species of *Scapter*, except *S. caesariatus* Eardley, 1996, *S. peringueyi* and those of the *S. nitidus* and *S. basutorum* species groups, in having a medio-longitudinally depressed clypeus ("mediolongitudinal sulcus" in Eardley 1996), but the depression is shallower than in the species of the *S. nitidus* and *S. basutorum* groups. With 6.8–9.3 mm body length, *S. heterodoxus* is on average larger than *S. caesariatus* (at most 7.3 mm) and the species of the *S. nitidus* group (at most 7.7 mm long). It differs from all aforementioned *Scapter* species except *S. peringueyi* in having a declivous propodeal surface, without a nearly horizontal basal zone. *Scapter heterodoxus* is very similar and clearly closely related to *S. peringueyi*. It differs in having a rugulose surface sculpturing of the basal zone of the propodeum, particularly of the anterior portion, whereas the sculpturing of *S. peringueyi* is substrigulate (Figs 5E, 5F).

As in the male, the integument between the punctation on the mesoscutum is polished in *S. heterodoxus* and shagreened (dull) in *S. peringueyi*.

Comments. The females of *S. heterodoxus* and *S. peringueyi* are difficult to distinguish at times, whereas the males are easily recognized. The published sequence data of *S. heterodoxus* from previous molecular-phylogenetic treatments (Almeida and Danforth 2009; Branstetter et al. 2017; Almeida et al. 2019) is associated with a vouchered specimen deposited in the CUIC. This specimen is part of the examined series listed under additional material, which was collected in the Western Cape Province, 31 km S of Clanwilliam. The voucher corresponds to the type specimen of *S. heterodoxus*, which means that the previously published DNA data refers to the true *S. heterodoxus* and not to *S. peringueyi*.

***Scapter peringueyi* (Cockerell, 1921), stat. rev.**

Figures 3–5

Polyglossa peringueyi Cockerell, 1921: 205.

Material examined. Holotype: South Africa: Knysna, C. C., October 1916, leg. L. Péringuey, ♀, SAMC. Additional material: South Africa: Knysna, C. C., October 1916, leg. L. Péringuey, ♀, SANC, Database No. HYMA04122. Cape Province, Hermanus, 34°24.76'S, 19°17.25'E, 28 September 2001, leg. B. N. Danforth, C. D. Eardley, K. L. Walker, 17 ♂, CUIC. Cape Province, Pearly Beach, Bredasdorp, September 1959, –34.6667, 19.51667, leg. South African Museum Expedition, 3♂ and 2♀, SAMC, cat. no. SAM-HYM-B007139. Cape Province, Pearly Beach, Bredasdorp, September 1959, –34.6667, 19.51667, leg. South African Museum Expedition, 41♂ and 5♀, SAMC, cat. no. SAM –HYM-B007773. Cape Province, Somerset (W.) Strand, 25 October 1925, –34.1167, 18.8333, leg. H. Brauns, 1♂, SAMC, cat. no. SAM-HYM-B007776b. Cape Province, Cape of Good Hope Nature Reserve, 18 September 1975, leg. V. B. Whitehead, 1♂ and 3♀, SAMC, cat. no. SAM-HYM-B007778. Cape Province, Cape of Good Hope Nature Reserve, Olifantsbos, near Skaife center, –34.2667, 18.3833, 18–19 September 1993, leg. S. van Noort, 1♀, SAMC, cat. no. SAM-HYM-B007779. Cape Province, Vermont, –34.4167, 19.1667, 10 October 1977, leg. V. B. Whitehead, 1♂, SAMC, cat. no. SAM-HYM-B007780. Cape Province, Knysna, October 1916, leg. L. Péringuey, 5♀, SAMC, cat. no. SAM-HYM-B007782. Cape Province, Hout Bay, opp. Duiker Is., –34.0333, 18.3, 11 October 1986, leg. K. Steiner, 1♀, SAMC, cat. no. SAM-HYM-B007783. Cape Province, Strandfontein, –34.0833, 18.5500, 1 November 1960, leg. F. W. Gess, 1♂, SAMC, cat. no. SAM-HYM-B007787. Cape Province, Cape of Good Hope Nature Reserve, 8 October 1986, leg. K. Steiner, 1♂, SAMC, cat. no. SAM-HYM-B009504. Cape Province, Hout Bay, Duiker Point, –34.0333, 18.3, 11 October 1986, leg. K. Steiner, 1♂, SAMC, cat. no. SAM-HYM – B009505.

Diagnosis. *Scapter peringueyi* is morphologically very similar to *S. heterodoxus*. ♂: the male of *S. peringueyi* differs from that of *S. heterodoxus* in the shape of the projecting apical portion of the hind tibia, which is parallel-sided (tapering in *S. heterodoxus*)



Figure 3. Female holotype of *Scrapter peringueyi* (Cockerell, 1921), stat. rev. (SAM-HYM-B000144). **A** habitus, dorsolateral view **B** habitus, lateral view **C** head, frontal view **D** propodeum **E** labels **F** fore wing.

(Figs 1E, 4E, 5A, 5B). It further differs from *S. heterodoxus* in the surface sculpturing of the basal zone of the propodeum, which is substrigulate in *S. peringueyi* and rugulose in *S. heterodoxus* (Figs 1D, 3D, 5C, 5D). The integument on the mesoscutum is shagreened between the punctuation, whereas it is polished in *S. heterodoxus*.

♀: the female of *S. peringueyi* differs from *S. heterodoxus* in the same characters as the male, except for the shape of the hind tibia. The surface sculpturing of the basal zone of the propodeum is substrigulate, whereas it is rugulose in *S. heterodoxus* (Figs 2D, 3D, 5E, 5F). The integument between the punctuation on the mesoscutum is shagreened in *S. peringueyi* and it is polished in *S. heterodoxus*.



Figure 4. Non-type male specimen of *Scapter peringueyi* (Cockerell, 1921), stat. rev. **A** habitus, dorsal view **B** habitus, lateral view **C** head, frontal view **D** propodeum **E** hind leg tibia **F** fore wing.

Discussion

Scapter heterodoxus and *S. peringueyi* were described as species by Cockerell in the same publication (Cockerell 1921). Subsequently, in his major revisionary work on *Scapter*, Eardley (1996) synonymized the two species and regarded only *Scapter heterodoxus* as valid. Thus, the *Scapter heterodoxus* species ‘group’ was regarded as monotypic over the past decades. In the present study, we reassess the status of both species using morphological and molecular methods, and find strong support for the re-recognition of *S. peringueyi*

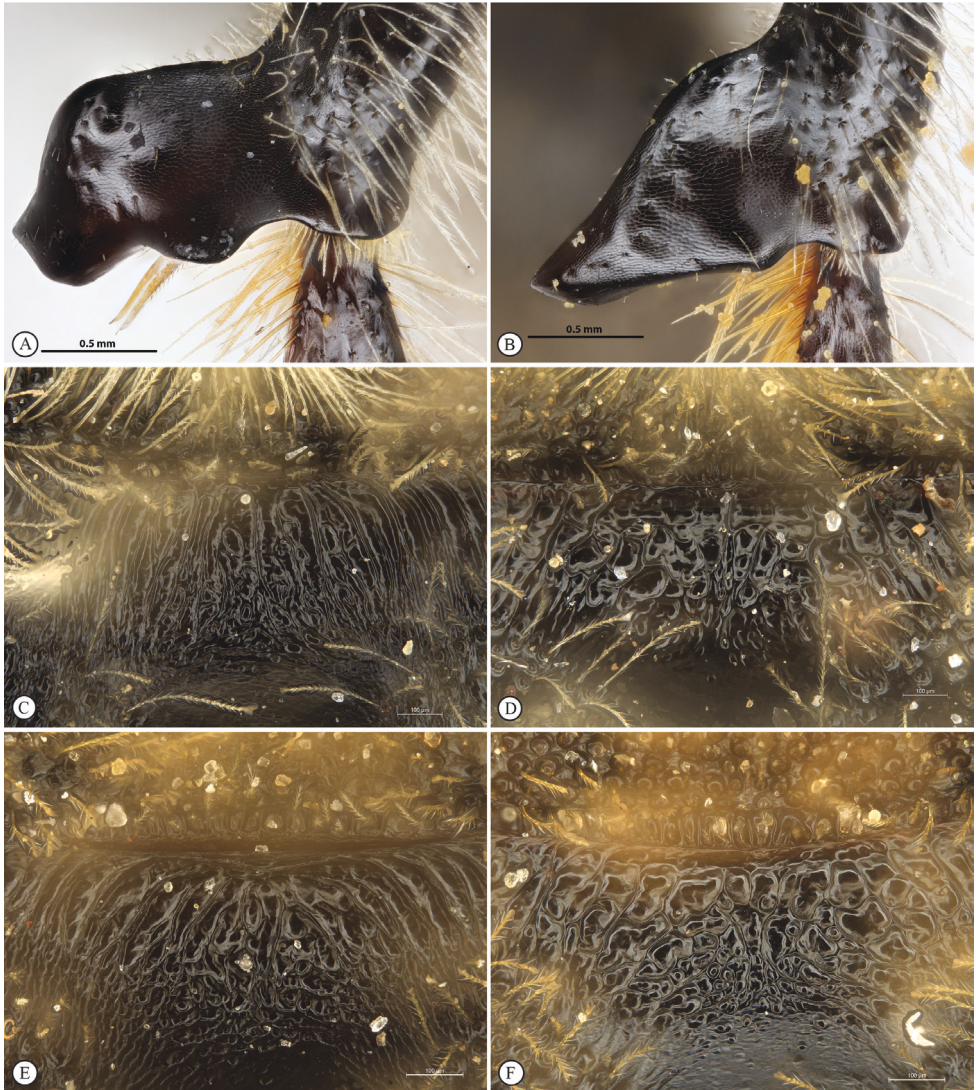


Figure 5. Comparison of the shape of the male hind leg tibia and propodeal sculpture. **A** *Scapter peringueyi* (Cockerell, 1921), stat. rev. hind leg tibial apex, non-type male specimen (deposited in CUIC) **B** *Scapter heterodoxus* (Cockerell, 1921) hind leg tibial apex, non-type male specimen (deposited in CUIC) **C** *Scapter peringueyi* (Cockerell, 1921), stat. rev. propodeal sculpture, non-type male specimen (SAM-HYM-B007139) **D** *Scapter heterodoxus* (Cockerell, 1921) propodeal sculpture, lectotype male (SAM-HYM-B000145) **E** *Scapter peringueyi* (Cockerell, 1921), stat. rev. propodeal sculpture, holotype female (SAM-HYM-B000144) **F** *Scapter heterodoxus* (Cockerell, 1921) propodeal sculpture, non-type female (SAM-HYM-B007786).

as a valid second species in the *Scapter heterodoxus* group. While both species are morphologically very similar, clearly closely related, and not particularly like any other species of *Scapter*, they can be readily separated using morphological characters and molecular

data. Differentiation of the species is particularly clear in the male sex based on the species-specific shape of the hind tibia (Fig. 5), which shows no intraspecific variation among the examined specimens or in illustrations in the literature (Brauns 1929; Eardley 1996). Other structures that are often diagnostic for species-recognition of *Scapter*, such as the genital capsule and terminal sterna, seem identical between the two species and cannot be used to separate *S. heterodoxus* and *S. peringueyi*. However, both sexes can also be separated by the different surface sculpturing of the basal zone of the propodeum and the polished or shagreened interspaces on the mesoscutum. These morphological differences that distinguish both males and females of *S. heterodoxus* from *S. peringueyi* allowed us to associate the female sex for both species, since we only generated COI sequence data from male individuals. In line with these morphological differences is the significant genetic distance between the examined specimens, which is 6.1% for the 657 base-pair long COI barcode region. Species delimitation based on pairwise genetic distances of this partial gene region is common practice in modern insect systematics and has been routinely applied for many insect groups such as Lepidoptera (e.g., Hausmann et al. 2011; Nneji et al. 2020), Coleoptera (e.g., Oba et al. 2015; Huang et al. 2020), Hymenoptera (e.g., Sheffield et al. 2009; Stahlhut et al. 2013), and specifically for certain African bees (Bossert et al. 2020). While the threshold for delimiting species boundaries is not universal, varies among studies, and is not ultimate proof, a distance of 2–3% is common practice to recognize a barcoding gap (Ratnasingham and Hebert 2013; Hebert et al. 2003; and references above). The calculated distance between *S. heterodoxus* and *S. peringueyi* exceeds such thresholds considerably, underlining the need to recognize them as distinct species.

Prior and subsequent to Eardley's (1996) revision of *Scapter* and the synonymization of *S. peringueyi* with *S. heterodoxus*, samples of '*Scapter heterodoxus*' have been included in a number of morphological-phylogenetic studies (Alexander and Michener 1995; Davies and Brothers 2006; Packer 2008; Mthethwa 2016; Plant and Paulus 2016; Porto and Almeida 2019), or assessments of pollinator communities (Tribe 2007; Goldblatt et al. 2009). As the distinguishing characters between *S. heterodoxus* and *S. peringueyi* are not specifically mentioned in these works, it is not immediately clear which of the two species were actually included in the respective studies. It is therefore possible that some of the examined specimens may in fact have corresponded to *S. peringueyi*. For example, the material examined in Mthethwa (2016) almost certainly consists of a mixed sample of both *S. heterodoxus* and *S. peringueyi*, since the specimens for morphological study were collected in Citrusdal and Hermanus. According to the distributional patterns discussed below, these collection localities make it very likely that both species were included. However, given the overall very similar, or seemingly identical shape of most examined morphological structures and the close evolutionary relationship of the two species, we do not expect that this combined interpretation could significantly impact results and conclusions of any of these phylogenetic studies. More care would need to be taken in assessing pollination networks, given that there may be disparity in host plant fidelity between the two species. Interestingly, the two species were confused early on: in one of the very first treatments of *S. heterodoxus* after Cockerell's description (Cockerell 1921), Brauns (1929) redescribed the species and illustrated the hindleg tibia based on a male specimen. The shape of the tibia, however, clearly corresponds to that of *S. peringueyi* (cf., Fig. 5A) and not of *S. heterodoxus*.



Figure 6. Distribution map of *Scapter peringueyi* (Cockerell, 1921) and *Scapter heterodoxus* (Cockerell, 1921) based on 133 examined specimens. If several specimens were collected at the same site, they are shown as a single occurrence.

Mapping the distributions of *S. peringueyi* and *S. heterodoxus* based on the 133 examined specimens reveals slightly different distribution patterns for the two species (Fig. 6). *Scapter peringueyi* is a southern Cape coastal species, without any records north of the Cape Town area. All localities are in close proximity to the shoreline, without any records from inland regions. *Scapter heterodoxus* in turn extends from Cape Town northwards up the south-western coast of South Africa, with most occurrences recorded from inland of the western coastline. The two species are sympatric in the Cape Town vicinity. Additionally, we recovered two isolated records for *S. heterodoxus*, one from the interior of the Eastern Cape (Katberg), and another one from Kakamas in the interior Northern Cape region. These records are particularly interesting as they significantly expand the distributional range of *S. heterodoxus*, but they also warrant further study: the surface sculpturing of these two specimens is slightly less rugulose than in the females from the Cape Town region, which is where the type locality is located. Additional study of specimens from the interior Northern and Eastern Cape regions is required to determine the degree of variation of this propodeal character and could possibly reveal additional, yet to be described species of the *S. heterodoxus* species group.

Acknowledgements

We thank Bryan N. Danforth (Cornell University) for providing us access to the specimens deposited in the Cornell University Insect Collection and Werner Strumpher (South African National Collection of Insects) for help in locating the type specimens. We thank the reviewers and the editorial team of *African Invertebrates* for their constructive feedback on the manuscript. This work was supported by U.S. National Science Foundation grants DEB-2127744 and DEB-0814544.

References

- Alexander BA, Michener CD (1995) Phylogenetic studies of the families of short-tongued bees (Hymenoptera: Apoidea). *The University of Kansas Science Bulletin* 55: 377–424.
- Almeida EAB, Danforth BN (2009) Phylogeny of colletid bees (Hymenoptera: Colletidae) inferred from four nuclear genes. *Molecular Phylogenetics and Evolution* 50(2): 290–309. <https://doi.org/10.1016/j.ympev.2008.09.028>
- Almeida EAB, Pie MR, Brady SG, Danforth BN (2012) Biogeography and diversification of colletid bees (Hymenoptera: Colletidae): emerging patterns from the southern end of the world. *Journal of Biogeography* 39(3): 526–544. <https://doi.org/10.1111/j.1365-2699.2011.02624.x>
- Almeida EAB, Packer L, Melo GAR, Danforth BN, Cardinal SC, Quintero FB, Pie MR (2019) The diversification of neopasiphaeinae bees during the Cenozoic (Hymenoptera: Colletidae). *Zoologica Scripta* 48(2): 226–242. <https://doi.org/10.1111/zsc.12333>
- Bankevich A, Nurk S, Antipov D, Gurevich AA, Dvorkin M, Kulikov AS, Lesin VM, Nikolenko SI, Pham S, Pribelski AD, Pyshkin AV, Sirotkin AV, Vyahhi N, Tesler G, Alekseyev MA, Pevzner PA (2012) SPAdes: A new genome assembly algorithm and its applications to single-cell sequencing. *Journal of Computational Biology* 19(5): 455–477. <https://doi.org/10.1089/cmb.2012.0021>
- Bossert S, Copeland RS, Sless TJL, Branstetter MG, Gillung JP, Brady SG, Danforth BN, Polcarová J, Straka J (2020) Phylogenomic and morphological reevaluation of the bee tribes Biastini, Neolarrini, and Townsendiellini (Hymenoptera: Apidae) with description of three new species of *Schwarzia*. *Insect Systematics and Diversity* 4(6): 1–29. <https://doi.org/10.1093/isd/ixaa013>
- Bossert S, Wood TJ, Patiny S, Michez D, Almeida EAB, Minckley RL, Packer L, Neff JL, Copeland RS, Straka J, Pauly A, Griswold T, Brady SG, Danforth BN, Murray EA (2021) Phylogeny, biogeography and diversification of the mining bee family Andrenidae. *Systematic Entomology*, 1–20. <https://doi.org/10.1111/syen.12530>
- Branstetter MG, Danforth BN, Pitts JP, Faircloth BC, Ward PS, Buffington ML, Gates MW, Kula RR, Brady SG (2017) Phylogenomic insights into the evolution of stinging wasps and the origins of ants and bees. *Current Biology* 27(7): 1019–1025. <https://doi.org/10.1016/j.cub.2017.03.027>
- Brauns H (1929) Neue und auffallende Apiden aus Süd-Afrika. *Zeitschrift für wissenschaftliche Insektenbiologie* 24: 130–143.
- Cardinal S, Buchmann SL, Russell AL (2018) The evolution of floral sonication, a pollen foraging behavior used by bees (Anthophila). *Evolution* 72(3): 590–600. <https://doi.org/10.1111/evo.13446>
- Cockerell TDA (1915) XXX.—Descriptions and records of bees.—LXVI. *Annals and Magazine of Natural History (Ser 8)* 15: 341–350. <https://doi.org/10.1080/00222931508693649>
- Cockerell TDA (1916) LI.—Descriptions and records of bees.—LXXII. *Annals and Magazine of Natural History (Ser 8)* 17: 428–435. <https://doi.org/10.1080/00222931608693809>
- Cockerell TDA (1921) XXV.—Descriptions and Records of Bees.—XC. *Annals and Magazine of Natural History (Ser 9)* 7: 201–212. <https://doi.org/10.1080/00222932108632512>

- Cockerell TDA, Ireland LM (1933) The relationships of *Scapter*, a genus of African bees. *Proceedings of the National Academy of Sciences of the United States of America* 19(11): 972–978. <https://doi.org/10.1073/pnas.19.11.972>
- Davies GBP, Brothers DJ (2006) Morphology of *Scapter* (Hymenoptera: Anthophila: Colletidae), with description of three new species and taxonomic status of five Cockerell taxa. *African Invertebrates* 47: 135–183.
- Davies GBP, Eardley C, Brothers DJ (2005) Eight new species of *Scapter* (Hymenoptera: Apoidea: Colletidae), with descriptions of *S. albifumus* and *S. amplispinatus* females and a major range extension of the genus. *African Invertebrates* 46: 141–179.
- Eardley CD (1996) The genus *Scapter* Lepeletier & Serville (Hymenoptera: Colletidae). *African Entomology* 4: 37–92.
- Eardley CD, Kuhlmann M, Pauly A (2010) The bee genera and subgenera of sub-Saharan Africa. *Abc Taxa* 7: 1–139.
- Edgar RC (2004) MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32(5): 1792–1797. <https://doi.org/10.1093/nar/gkh340>
- Faircloth BC (2016) PHYLUCE is a software package for the analysis of conserved genomic loci. *Bioinformatics* 32(5): 786–788. <https://doi.org/10.1093/bioinformatics/btv646>
- Fries H (1909) Die Bienen Afrikas nach dem Stande unserer heutigen Kenntnisse. In: Schultze, L (Ed.) *Zoologische und Anthropologische Ergebnisse einer Forschungsreise im Westlichen und Zentralen Südafrika ausgeführt in den Jahren 1903–1905*, Band 2. *Denkschriften der Medizinisch-Naturwissenschaftlichen Gesellschaft zu Jena* 14: 83–476. <https://doi.org/10.5962/bhl.title.10343>
- Fries H (1912) Neue und wenig bekannte Bienen Süd-Afrikas. (Hym.). *Archiv für Naturgeschichte* 78A: 181–189.
- Fries H (1913) II. Nachtrag zu ‘Bienen Afrika’. *Zoologische Jahrbücher* 35: 581–598. <https://doi.org/10.5962/bhl.part.16721>
- Goldblatt P, Manning JC, Nänni I (2009) New species of *Geissorhiza* (Iridaceae: Crocoideae) from the southern African winter rainfall zone, range extensions, taxonomic changes, and notes on pollen morphology and floral ecology. *Bothalia* 39(2): 123–152. <https://doi.org/10.4102/abc.v39i2.240>
- Harris RA (1979) A glossary of surface sculpturing. *Occasional Papers in Entomology, State of California Department of Food and Agriculture* 28: 1–31.
- Hausmann A, Haszprunar G, Hebert PD (2011) DNA barcoding the geometrid fauna of Bavaria (Lepidoptera): Successes, surprises, and questions. *PLoS One* 6(2): e17134. <https://doi.org/10.1371/journal.pone.0017134>
- Hebert PDN, Ratnasingham S, de Waard JR (2003) Barcoding animal life: Cytochrome c oxidase subunit 1 divergences among closely related species. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 270(Supplement): S96–S99. <https://doi.org/10.1098/rsbl.2003.0025>
- Huang W, Xie X, Huo L, Liang X, Wang X, Chen X (2020) An integrative DNA barcoding framework of ladybird beetles (Coleoptera: Coccinellidae). *Scientific Reports* 10(1): 10063. <https://doi.org/10.1038/s41598-020-66874-1>

- Kayaalp P, Stevens MI, Schwarz MP (2017) ‘Back to Africa’: Increased taxon sampling confirms a problematic Australia-to-Africa bee dispersal event in the Eocene. *Systematic Entomology* 42(4): 724–733. <https://doi.org/10.1111/syen.12241>
- Kuhlmann M (2009) Patterns of diversity, endemism and distribution of bees (Insecta: Hymenoptera: Anthophila) in southern Africa. *South African Journal of Botany* 75(4): 726–738. <https://doi.org/10.1016/j.sajb.2009.06.016>
- Kuhlmann M (2014) Revision of the “euryglossiform” species of the Afrotropical bee genus *Scapter* Lepeletier & Serville, 1828 (Hymenoptera: Apoidea: Colletidae). *European Journal of Taxonomy* 95(95): 1–69. <https://doi.org/10.5852/ejt.2014.95>
- Kuhlmann M, Eardley CD (2012) Pollen resources of non-*Apis* bees in southern Africa. In: Patiny S (Ed.) *Evolution of Plant-Pollinator Relationships*. Cambridge University Press, Cambridge, United Kingdom, 439–457. <https://doi.org/10.1017/CBO9781139014113.017>
- Kuhlmann M, Friehs T (2020) Nine new species and new records of euryglossiform *Scapter* Lepeletier & Serville (Hymenoptera: Colletidae) from South Africa. *European Journal of Taxonomy* 647(647): 1–33. <https://doi.org/10.5852/ejt.2020.647>
- Kuhlmann M, Guo D, Veldtman R, Donaldson J (2012) Consequences of warming up a hotspot: Species range shifts within a centre of bee diversity. *Diversity & Distributions* 18(9): 885–897. <https://doi.org/10.1111/j.1472-4642.2011.00877.x>
- Lepeletier de Saint Fargeau ALM, Audinet-Serville JG (1828) In: Diderot et al. (Eds) *Encyclopedie Méthodique, Histoire Naturelle. Insectes*, Vol. 10. Agasse, Paris, 345–832.
- McGinley RJ (1981) Systematics of the Colletidae based on mature larvae with phenetic analysis of apoid larvae. *University of California Publications in Entomology* 91: 1–307.
- Michener CD (1944) Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). *Bulletin of the American Museum of Natural History* 82: 151–326.
- Michener CD (1997) Genus-group names of bees and supplemental family-group names. *Scientific Papers, Natural History Museum. The University of Kansas* 1: 1–81. <https://doi.org/10.5962/bhl.title.4052>
- Michener CD (2007) *The Bees of the World*. Second Edition. The Johns Hopkins University Press, Baltimore, Maryland, 953 pp.
- Mthethwa QM (2016) The taxonomy and systematics of the bee genus *Scapter* (Colletidae: Colletinae: Scaptrini). MSc dissertation: University of KwaZulu-Natal, 69 pp. <https://researchspace.ukzn.ac.za/handle/10413/15817> [Accessed July 30, 2021]
- Nneji LM, Adeola AC, Ayoola AO, Oladipo SO, Wang YY, Malann YD, Anyaele O, Nneji IC, Rahman MM, Olory CS (2020) DNA barcoding and species delimitation of butterflies (Lepidoptera) from Nigeria. *Molecular Biology Reports* 47(12): 9441–9457. <https://doi.org/10.1007/s11033-020-05984-5>
- Oba Y, Ôhira H, Murase Y, Moriyama A, Kumazawa Y (2015) DNA Barcoding of Japanese Click Beetles (Coleoptera, Elateridae). *PLoS One* 10(1): e0116612. <https://doi.org/10.1371/journal.pone.0116612>
- Packer L (2008) Phylogeny and classification of the Xeromelissinae (Hymenoptera: Apoidea, Colletidae) with special emphasis on the genus *Chilicola*. *Systematic Entomology* 33(1): 72–96. <https://doi.org/10.1111/j.1365-3113.2007.00398.x>

- Plant JD, Paulus HF (2016) Evolution and phylogeny of bees – a review and a cladistic analysis in light of morphological evidence (Hymenoptera, Apoidea). *Zoologica* 161: 1–364.
- Porto DS, Almeida EAB (2019) A comparative study of the pharyngeal plate of Apoidea (Hymenoptera: Aculeata), with implications for the understanding of phylogenetic relationships of bees. *Arthropod Structure & Development* 50: 64–77. <https://doi.org/10.1016/j.asd.2019.04.002>
- Ratnasingham S, Hebert PDN (2013) A DNA-based registry for all animal species: the Barcode Index Number (BIN) system. *PloS One* 8(8): e66213. <https://doi.org/10.1371/journal.pone.0066213>
- Sandhouse GA (1943) The type species of the genera and subgenera of bees. *Proceedings of the United States National Museum* 92(3156): 519–619. <https://doi.org/10.5479/si.00963801.3156.519>
- Sheffield CS, Hebert PDN, Kevan PG, Packer L (2009) DNA barcoding a regional bee (Hymenoptera: Apoidea) fauna and its potential for ecological studies. *Molecular Ecology Resources* 9: 196–207. <https://doi.org/10.1111/j.1755-0998.2009.02645.x>
- Shorthouse DP (2010) SimpleMappr, an online tool to produce publication-quality point maps. <http://www.simplemappr.net> [Accessed October 20, 2021]
- Stahlhut JK, Fernández-Triana J, Adamowicz SJ, Buck M, Goulet H, Hebert PDN, Huber JT, Merilo MT, Sheffield CS, Woodcock T, Smith MA (2013) DNA barcoding reveals diversity of Hymenoptera and the dominance of parasitoids in a sub-arctic environment. *BMC Ecology* 13(1): 1–13. <https://doi.org/10.1186/1472-6785-13-2>
- Tribe G (2007) Fruit crops: deciduous fruit in South Africa. African Pollinators Initiative (Producers) Crops, Browse and Pollinators in Africa: an Initial Stock-taking. Food and Agricultural Organization of the United Nations, Rome, Italy, 14–19.
- Vachal J (1897) Éclaircissements sur de genre *Scapter* et description d'une espèce nouvelle de *Dufourea*. *Bulletin de la Société Entomologique de France* 1897: 61–64. <http://dx.doi.org/10.3406/bsef.1897.21997>

Supplementary material I

Multiple sequence alignment of the examined species of *Scapter*

Authors: Silas Bossert

Data type: multiple sequence alignment

Explanation note: Multiple sequence alignment of the *Scapter heterodoxus* and *Scapter peringueyi* sequences analyzed in the present study. The alignment file is in Fasta format.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/AfrInvertebr.63.76934.suppl1>

Supplementary material 2

Specimen metadata

Authors: Simon van Noort, Silas Bossert

Data type: occurrences

Explanation note: Specimen metadata for the 133 examined specimens in Darwin Core format.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/AfrInvertebr.63.76934.suppl2>